

## STRUCTURE AND REPRODUCTION IN *LENORMANDIOPSIS NOZAWAE* (RHODOMELACEAE, RHODOPHYTA)

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**ABSTRACT.** — Four species of *Lenormandiopsis* Papenfuss have been described; the type species, *L. latifolia* (Harvey et Greville) Papenfuss, from Australia, *L. lorentzii* (Weber-van Bosse) Papenfuss, from Indonesia, Japan, Australia and Natal, *L. parthasarathii* (Krishnamurthy) Krishnamurthy from south India and *L. nozawae* R.E. Norris, from Natal. Tetrasporophytes are known for all four species, but females are known for only *L. lorentzii*, *L. parthasarathii* and *L. latifolia*. A recent collection of *L. nozawae* has provided additional information on its structure and reproduction including the first description of male and female reproductive organs. New information is also provided on the structure of tetrasporangial branches in *L. nozawae*, and comparison of these structures with those in other species and *Amansieae* genera is provided.

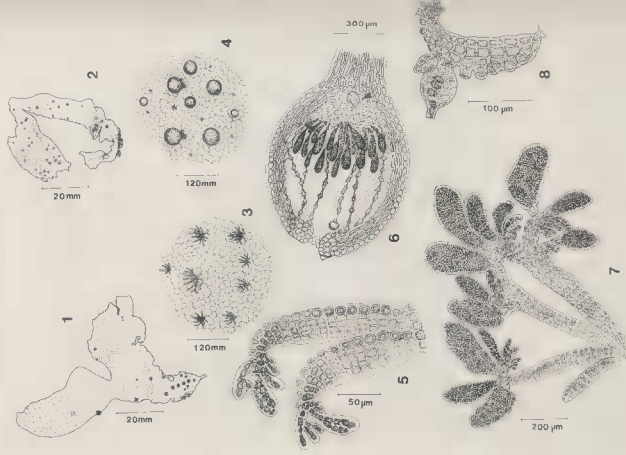
**RÉSUMÉ.** — Quatre espèces de *Lenormandiopsis* ont été décrites : l'espèce-type *L. latifolia* (Harvey et Greville) Papenfuss, d'Australie; *L. lorentzii* (Weber-van-Bosse) Papenfuss, d'Indonésie, du Japon, d'Australie et du Natal; *L. parthasarathii* (Krishnamurthy) Krishnamurthy, du sud de l'Inde; *L. nozawae* R.E. Norris, du Natal. Les tétrasporophytes sont connus chez ces quatre espèces, mais les gamétophytes femelles ne sont connus que chez *L. lorentzii*, *L. parthasarathii* et *L. latifolia*. Une collection récente de *L. nozawae* a fourni des informations complémentaires sur sa structure et sur sa reproduction; les organes reproducteurs mâles et femelles sont décrits pour la première fois, et des précisions sont aussi données sur la structure des rameaux tétrasporifères. Ces structures sont comparées à celles des autres espèces de *Lenormandiopsis* et de certains genres d'*Amansieae*. (traduit par la rédaction).

**KEY WORDS :** *Lenormandiopsis*, morphology, Rhodophyceae, reproduction, Rhodomelaceae.

### INTRODUCTION

*Lenormandiopsis* Papenfuss (1967), formerly known as *Aneuria* Weber-van Bosse (1911), belongs to the *Amansieae*, a tribe in the Rhodomelaceae that has primary dorsiventrality expressed by inrolled branch apices and trichoblasts that are formed in a regular series, unilaterally along the primary axis, on the convex

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side. *Lenormandiopsis* has large, deeply lobed or unbranched thalli comprised of polysiphonous axes, but without a conspicuous midrib, and having broadly expanded lateral wings that are formed from divisions of four lateral pericentral cells (WEBER-VAN BOSSE, 1911; OKAMURA, 1929; NORRIS, 1987). The fifth pericentral cell is ventral and segments bearing trichoblasts have the trichoblast basal cell (eventually becoming the scar cell) embedded between the two dorsal pericentral cells. A single layer of cortical cells is formed on the broad surfaces of the pericentral cells and their medullary derivatives.

Specimens of *Lenormandiopsis* are rarely found, and little is known about early stages in development of thalli or its reproductive stages. Previous studies on *Lenormandiopsis* provide little detail on development of thalli and report mainly on tetrasporophytes. Female plants were reported by NOZAWA (1965), KRISHNAMURTHY (1967) and NORRIS (1987). Male plants were described only for *L. parthasarathii* (Krishnamurthy) Krishnamurthy in Krishnamurthy et Joshi (1970) by KRISHNAMURTHY (1967).

A recent collection of specimens of *L. nozawae* R.E. Norris from northern Natal has provided plants in all phases of reproduction. The knowledge gained from a study of these plants and their reproductive organs is provided in addition to more complete information on development of thalli and the special reproductive branchlets in this genus.

## MATERIALS AND METHODS

The collection of *Lenormandiopsis nozawae* (Natal Benthic Algal Research Program (Nat) n° 4132) came from 2.5 km offshore from Sodwana Bay, northern Natal. Specimens were found by divers, J. Dench and D. Smith, at a depth of 56 m occurring on stable sand. The dive was made on 16-V-1986 through the auspices of the Natal Parks Board. Specimens were fixed in 5% formalin in seawater and returned to the laboratory where they were examined and processed for herbarium sheets (NU 9722, 9724- tetrasporophytes, NU 9725- male and female) and microscope slides, the latter prepared by mounting in aniline blue stained corn syrup mounting medium (MIN-THEIN and WOMER-SLEY, 1976).

Fig. 1. Male thallus of *Lenormandiopsis nozawae* (NU 9725). The large clusters of dark material represent pustulate callus-like tissue that may be eroded parasites. Small distal spots on the left lobe represent sori of male branchlets. Fig. 2. Female thallus of *Lenormandiopsis nozawae* (NU 9725) on which are distributed stalked cystocarps. Fig. 3. Slightly magnified fertile region of male thallus showing sori of male branchlets. Fig. 4. Slightly magnified fertile region of a female thallus showing sori of female branchlets and stalked cystocarps. Fig. 5. Two young male branchlets showing dorsal row of scar cells and distal trichoblasts. Fig. 6. Section of a cystocarp. Note large cells (arrowhead) at base of pseudoparenchymatous gonimoblast and sterile gonimoblast filaments following inner contour of the pericarp. Fig. 7. Male branchlets bearing spermatangia. Note that the two right-hand branchlets are branched. Fig. 8. Female branchlet bearing two procarpal branchlets. Note that these fertile branchlets replace trichoblasts in the middle region of the branchlet.

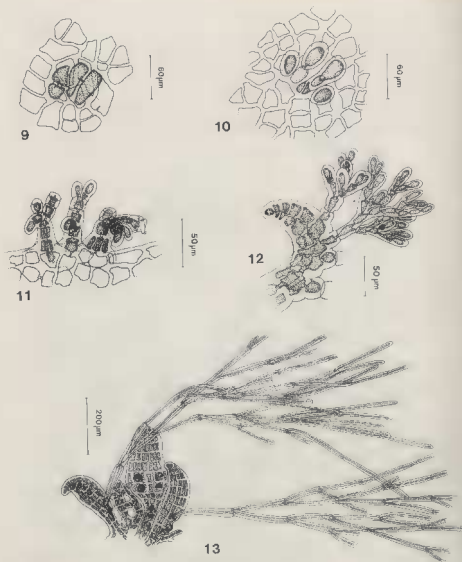


Fig. 9. Embedded periclinal branchlet, at a very early stage of development, from which upright tetrasporangial branchlets originate. Cortical cells of the thallus cover the branchlet at this stage. Fig. 10. First cells of erect branchlets arising from the embedded cells of a branchlet similar to the one shown in Fig. 9. Fig. 11. Section of cortex showing erect branchlets in a tetrasporangial sorus at an early stage of development. Note that scar cells have formed on all three branchlets. Fig. 12. Distal part of a young tetrasporangial branchlet showing highly branched trichoblasts. The curved distal end, having no trichoblasts, probably is an early developmental stage in the formation of a stichidium. Fig. 13. Several young tetrasporangial branchlets, two of them bearing highly branched mature trichoblasts.

## RESULTS

Two gametophyte and two tetrasporophyte specimens of *L. nozawae* were found in the collection. It was fortunate that a gametophyte of each sex was present, both specimens being apparently mature but small (both specimens are approximately 8 cm long) and having a somewhat distorted shape (Figs. 1, 2). A tetrasporophyte present in this collection (Fig. 14) is the most complete and largest specimen known for this rare species, being approximately 38 cm long and 12 cm broad in its largest dimension. This tetrasporophyte shows a growth form indicating it is a perennial plant in having a branched basal stipitate section, each branch of which terminates in a broad blade, presumably of seasonal growth. The proximal stipitate part of this plant probably originated by secondary thickening of axes along with erosion of the lateral winged regions.

These observations strongly suggest that gametophytes and tetrasporophytes are heteromorphic in *L. nozawae*, but further collections of gametophytes are needed before such a conclusion can be substantiated. There was no suggestion of heteromorphy between tetrasporophytes and female gametophytes described for *L. lorentzii* (NOZAWA, 1965) nor for the type species of *Lenormandiopsis*, *L. latifolia* (NORRIS, 1987). KRISHNAMURTHY (1967), however, mentioned that the tetrasporophytes of *L. parthasarathi* are more robust than the gametophytes of that species.

Male and female reproductive structures are borne on fertile cylindrical polysiphonous branchlets in clusters (small sori) in no particular pattern on both surfaces of the blades (Fig. 3, 4).

The region of apical growth of *L. nozawae* was illustrated and described by NORRIS (1987) showing early development of the blade and the conspicuous row of trichoblasts, soon becoming scar cells, that is produced only by cells of the primary axis. Male and female fertile branchlets develop a trichoblast for each branch segment, whereas tetrasporangiate branchlets have scar cells only in a few proximal segments below the swollen part that bears the tetrasporangia. (This swollen tetrasporangial-bearing part of the branchlet may be termed a *stichidium* in the sense of the definition provided by ABBOTT and HOLLENBERG (1976), in which only tetrasporangial-bearing branchlets are designated by this term. The term has also been used by various authors in a broader sense to include male reproductive branchlets in a wide variety of red algal genera).

Trichoblasts, occurring on primary vegetative and endogenous fertile branches, are colourless and often unicellular in *Lenormandiopsis* (NORRIS, 1987). Trichoblasts on fertile branchlets may be unicellular or multicellular and highly branched (Figs. 12, 13). In both vegetative and fertile branches of *Lenormandiopsis* trichoblasts originate as the first derivative of an axial cell, the initial being cut off on the convex (dorsal) side as a small protuberant cell, a process termed exogenous in the Rhodomelaceae (ABBOTT & HOLLENBERG, 1976). The branched trichoblasts have a form typical for some genera of the Amansieae (*Rytiplalea*, *Amansia* and *Vidalia* according to FALKENBERG (1901)) in that

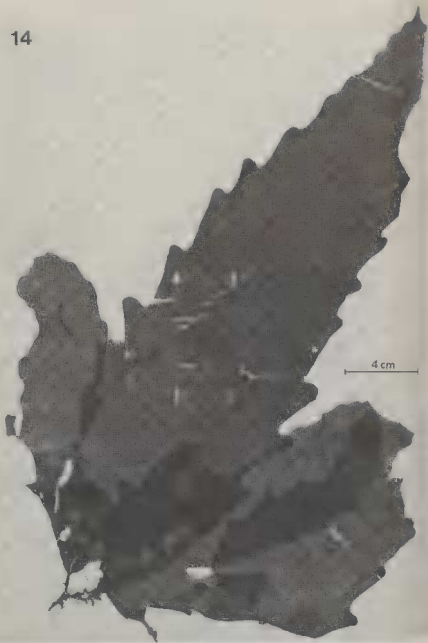


Fig. 14. Thallus of a large tetrasporophyte of *Lenormandiopsis nozawae* (NU 9722) showing the branched perennial stipe, each branch terminating in a blade. The central large tapered blade has evenly spaced marginal lobes typical for this species.

they become fully formed at an early stage inside a vesicle comprised of apparently liquid wall material that envelopes all cells of the trichoblast. The vesicle has a thin membrane (cuticle) that bursts leaving remains of the cuticle attached to the internal stalk cell, and an envelope reforms around the cell contours of the trichoblast. At this stage the trichoblast cells rapidly enlarge, expanding to form a monosiphonous highly branched filament that soon is deciduous leaving a large conspicuous scar cell, partly submerged in the thallus, which is the stalk cell of the original trichoblast.

As mentioned above, trichoblasts may be very simple in *Lenormandiopsis*, often represented by two cells, an interior stalk cell and a terminal cell, the latter being deciduous and the stalk cell remaining as a scar cell, a cell that has protuberant wall material, obviously severed from another cell. Scar cells, whether derived from single-celled or multicellular trichoblasts, all have the same structure. In young parts of the thallus scar cells can be identified in every segment in *Lenormandiopsis*, but in more proximal regions of thalli, under the influence of intercalary cell divisions, they are difficult to find.

Thallus primary and secondary axes are identifiable in distal regions near the inrolled branch apex but soon lose their identity because there is no development of special cortication around them. Apices of secondary branches can be identified at tips of conical shallow lobes on margins of some thalli (Fig. 14). In young parts of the thallus apex some of the secondary branch apices may support a single cylindrical or slightly flattened marginal sterile branch. The primary axis of this branch sometimes bears a series of scar cells, representing broken off trichoblasts, and the number of pericentral cells is variable but usually more than five. Such marginal branches are not always formed, and their very small size and deciduous nature also make them difficult to find. Thallus proliferations may occur on torn margins and small adventitious thalli sometimes develop on stipes of adult thalli (Fig. 14).

### Ontogeny and structure of fertile branchlets :

Clusters of endogenously derived fertile branchlets are formed in no apparent order on both thallus surfaces. At first investigation it was thought that the fertile branchlet clusters developed on axes (NORRIS, 1987), but this cannot be substantiated by subsequent investigations. It is now concluded that they occur in no special arrangement although the clusters of branchlets are fairly regularly spaced. It also seems evident that fertile branchlet clusters can be initiated even in fully mature regions of the thallus. Ontogeny of the branchlet cluster (sorus) has been studied in a tetrasporophyte of *L. nozawae*. In this plant the initiation of a branchlet cluster, as observed from the thallus surface, occurs by cutting off of a short curved row of cells (Fig. 9) from a medullary cell of the thallus. The first branchlet, which is orientated periclinally, is embedded beneath the cortex and upright branchlets that penetrate the cortex are initiated from each cell of the embedded branchlet (Fig. 10). All of the initial branchlets are monosiphonous, but the protuberant ones soon become poly-

siphonous (Fig. 11). Divisions of cells in the basal region of the protuberant branchlets, as well as divisions of the original embedded branchlet, cause a small and relatively thin erumpent mass of tissue to develop from which emerge many upright polysiphonous branchlets, each beginning as a monosiphonous filament. In this way the clusters of fertile branchlets are formed and sterile branchlets have not been identified with certainty in these sori. Each fertile branchlet in tetrasporophyte, male or female plants is dorsiventral, determinate, and produces five pericentral cells in each segment in addition to the stalk cell of a dorsal trichoblast, the cell that becomes a scar cell when the trichoblast is lost. Proximal and distal axial cells in the fertile branchlet may have fewer corticating or pericentral cells, or occasionally none, resulting in fertile branchlets that are tapered at both distal and proximal ends.

**Male branchlets :** Male fertile branchlets bear a series of dorsal trichoblasts in early stages (Fig. 5), but as the fertile branchlet matures it continues the series by forming trichoblasts transformed into spermatangial branchlets (Fig. 7). Each spermatangial branchlet has a small stalk cell inserted between pericentral cells of the fertile branchlet, comparable to the stalk cell of the trichoblast, and an enlarged external stalk cell. The spermatangial branchlet represents the complete highly branched trichoblast condensed to a small unit having a dorsiventral aspect in which the dorsal internal branchlets are longer than those in ventral positions. No terminal sterile cells are present in the spermatangial branchlet, all surface cells being fertile (Fig. 7). Male polysiphonous branchlets of *L. nozawae* may have one or two secondary polysiphonous branchlets that develop endogenously on segments in addition to trichoblasts or spermatangial branchlets (Fig. 7). There appears to be no particular order in the development of these secondary branchlets of the polysiphonous axis.

**Female branchlets :** Fertile branchlets on female plants (Fig. 8) are similar in appearance, in early stages, to those on male plants. They have a polysiphonous structure that tapers to a narrow proximal stalk that becomes greatly thickened by cortication (Fig. 4) as cystocarps develop. Procarps with their pericarp initials are produced in place of trichoblasts in proximal to middle positions on the fertile branchlet, only one or two such procarys being produced on each branchlet. Because female reproductive branchlets replace trichoblasts, as spermatangial branchlets do in male branchlets, it can be assumed that the two branchlets are basically the same, the female branchlet differing in having a polysiphonous distal segment. Usually only a single cystocarp develops in each cluster of fertile branchlets (Fig. 4), but occasional twinned cystocarps can be found on the same stalk. The cystocarp stalk is the proximal segment of the fertile branchlet that becomes greatly thickened by cortication.

An apical protuberant cell is present on the distal part of the young pericarp before fertilization, which probably represents a sterile cell of the trichoblast that bears the procarpial structure. The stalk of the procarpial branch is polysiphonous having four or five pericentral cells. Few stages in early development of cystocarps were observed but the four-celled carpogonial branch was seen. It



could not be determined if there are one or two groups of sterile cells attached to the supporting cell. It may be assumed for the present, however, that two groups are present, a situation similar to the procarp structure reported by NOZAWA (1965) for *L. lorentzii*.

A significant difference exists in the structure of the female fertile branchlets reported by Nozawa for *L. lorentzii* and those found in *L. nozawae*. Nozawa showed the fertile branchlet to be terminated by a trichoblast and she did not show nor discuss the scar cells that should be present on the dorsal side of the fertile branchlet in that species. The fertile female branchlet structure of *L. lorentzii* probably is similar to that of *L. nozawae* and *L. latifolia*, the latter previously reported by NORRIS (1987). In my estimation, it is basic in the genus, and possibly the Amansieae, that scar cells are present on the dorsal side of endogenous branchlets, and in gametophytes the branchlet terminates in an apical cell that first exogenously produces a trichoblast or a fertile branchlet on every segment. Tetrasporangial stichidia usually have no trichoblasts formed in the fertile region, but exceptions in the Amansieae can be cited (*i.e.* a few lower fertile segments in *L. lorentzii* and in all segments of stichidia in *Kuetzingia natalensis*). The number of procarps produced on each fertile branchlet in *L. lorentzii* is up to four, as reported by Nozawa, whereas one or two are known to occur on fertile branchlets of *L. nozawae*. An important feature of *Lenormandiopsis* cystocarps is that a fusion cell was not observed in *L. lorentzii* by Nozawa nor was one found in cystocarps of *L. nozawae*. KRISHNAMURTHY (1967), however, stated that fusion cells are present in cystocarps of *L. parthasarathii*. NOZAWA (1965) mentioned that the lower region of the gonimoblast in *L. lorentzii* is pseudoparenchymatous. Large fusion cells are found in most species of Rhodomelaceae so the possible absence of one in some species of *Lenormandiopsis* is particularly interesting and significant. It may be that a very small fusion cell is produced in *L. nozawae*, as shown in Fig. 6, but several separate large cells rather than a fusion cell are present in some other cystocarps. In other ways the cystocarps of *Lenormandiopsis* species seem to be much the same. The peculiar gonimoblast filaments that form a loose tissue lining the inner side of the cystocarp (Fig. 6) is present in *L. nozawae* and *L. latifolia* but was not mentioned as being present in *L. parthasarathii* by KRISHNAMURTHY (1967).

**Tetrasporangial branchlets** : Fertile branches bearing tetrasporangia in *L. nozawae* have two sections, a proximal narrow polysiphonous region and a distal longer and wider section in which the tetrasporangia are borne (Fig. 13), the distal region being termed the stichidium. The proximal section has scar cells on each segment whereas no scar cells are present on the distal section (in one branch a scar cell was found on the proximal segment of the stichidium). Trichoblasts never have been found terminating the distal section of the tetrasporangial branchlet. Because of the absence of scar cells and trichoblasts on the distal section of the fertile branch, the region bearing the tetrasporangia, I interpret this area as a region similar to the male and female branches but without the corresponding stalk cells. In *L. nozawae*, therefore, the fertile tetrasporangial

branch represents a sessile single distal tetrasporangial stichidium, in which fertile and sterile cells are present in a predictable pattern according to their development, with a proximal sterile segment that bears scar cells, a segment functioning as a stichidial stalk. Both the stichidium bearing tetrasporangia and the male and female fertile branchlets are dorsiventrally orientated, each having curved distal ends and stronger development of cells on the dorsal side causing a general curve to the branch.

KRISHNAMURTHY (1967) mentioned that reproductive branchlets of gametophytes in *L. parthasarathii* are borne «in two alternating series along the convex surface of the recurved branch». These structures in *L. nozawae*, as well as in *L. latifolia*, are in a single series on the convex side of the branchlet but in some places their pit connections may alternate their attachment to the left or right sides of the adaxial cell. Trichoblasts in the latter two species are also always in a single series that may slightly alternate positions according to attachment points on the axial cell.

Tetrasporangial branchlets in *L. latifolia* and *L. lorentzii* have a structure identical to that of *L. nozawae*. In these species also, therefore, the stalk segment of the branchlet bears scar cells on each segment and represents a branchlet that bears a single sessile stichidium in which scar cells are absent and in which no terminal trichoblasts are found. Scar cells occasionally occur on one or two lower segments of the stichidial part of the branch, identified by a slightly larger diameter than the proximal region, this tendency being more common in *L. lorentzii* than in the other two species.

## DISCUSSION

Discovery of gametophytes of *L. nozawae* and the reinvestigation of tetrasporophytes have allowed a more complete description of this species and, in addition, have provided a better understanding of the genus. Male reproductive structures are typical for the Amansieae and procarpial and cystocarpic structures are similar to *L. lorentzii*, *L. parthasarathii* and *L. latifolia*. The production of sexual reproductive structures on special fertile branchlets in clusters on the blade also provides a basis for speculation on phylogenetic links within the Amansieae. Tetrasporangial fertile branchlets also show structure, revealed by the presence of trichoblasts on the proximal segments, suggesting that they may be produced in much the same way as the gametangia but, because of their sessile position on the fertile branch, this relationship has been more obscure.

Position and type of trichoblasts produced in *Lenormandiopsis*, all cells being preformed in a vesicle that bursts as the cells mature, relates this genus with *Rytiphlaea*, *Amansia* and *Vidalia*, a group within the Amansieae delimited on this character by FALKENBERG (1901). Because of the expansive nature of the thallus, *Lenormandiopsis* probably is more closely related to *Amansia* and *Vidalia* rather than to *Rytiphlaea*. The presence of simple cortication on the thallus separates *Lenormandiopsis* from *Amansia* and the thin cortication and

expansive blade without conspicuous veins seem to set the genus well apart from *Vidalia*. It is concluded, therefore, that *Lenormandiopsis* is a genus having characters that separate it from other genera in the Amansieae but recognizing that there is little detailed knowledge of structure and reproduction in this tribe and that with new information additional taxonomic reorganization may be necessary.

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